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A SYNOPSIS OF NEOTROPICAL HYLID FROGS, GENUS *OSTEOCEPHALUS*

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When we initiated a study of the herpetofauna at Santa Cecilia in Amazonian Ecuador in 1966, we were immediately confronted with many kinds of animals that we could not identify with the existing literature. Comparisons of our specimens with those preserved in other museums resolved some of the problems, but many identifications could be made only after study of type specimens; even then some determinations remained questionable. We now find that in order to prepare a meaningful account of the herpetofauna of Santa Cecilia, we must complete several taxonomic studies, the limits of which extend far beyond eastern Ecuador. Because of our interests in hylids we have begun our studies on these frogs.

One of us (Trueb, 1970a) studied the cranial osteology of casque-headed hylid frogs and redefined the genus *Osteocephalus* but did not determine the number of species in the genus. Our work in Amazonian Ecuador resulted in the discovery of the sympatric occurrence of three species at each of two localities; one of these species was found with a fourth species at another locality. Study of museum specimens confirmed the recognition of these four species in the Amazon Basin and lower Amazonian slopes of the Andes. A fifth species from Bolivia and Perú also is included in the genus. Examination of museum specimens has provided data on the geo-

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graphic variation in, and distribution of, the five species. However, our conclusions pertaining to some populations need substantiation, because we have been hampered by inadequate material from areas beyond Ecuador. More than half of the 905 specimens of *Osteocephalus* are from Ecuador, a relatively small part of the total range of the genus.

In this paper we are presenting a taxonomic review of the genus *Osteocephalus;* of necessity our study has been at the alpha level. We have utilized all of the usual external characters, as well as osteological features in our definitions of the species. Tadpoles and mating calls are available for only one species, *O. verrucigerus* (Trueb and Duellman, 1970); these and other important systematic characters, such as karyotypes, are not available for the group at this time. Our tendency has been to take a conservative view of species; thus it is doubtful that any subsequent worker will recognize fewer species in the genus. Our observations on these frogs in Amazonian Ecuador are presented in a final section of this paper.

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sincere thanks to all of these persons for their contributions to our endeavors.

MATERIALS AND METHODS

We have examined 893 preserved frogs, including the type specimens of all included nominal taxa, 8 skeletons, 1 lot of eggs, and 3 lots of tadpoles that we refer to the genus *Osteocephalus;* in addition skulls were removed from five preserved specimens, and radiographs were made of 12 other preserved specimens. We have been fortunate in seeing living individuals of all species, except *O. pearsoni,* but we have colored photographs of a living specimen of that species. Figures 1 and 2 were drawn from projected colored transparencies of living frogs. Terminology follows that of Duellman (1970b). On the distribution maps solid symbols indicate localities from which we have examined specimens ;open symbols represent additional locality records based on the literature. Throughout the text specimens are listed by their catalogue numbers preceded by the appropriate museum abbreviation, as follows:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
ASU	Arizona State University
AUM	Auburn University Museum
BMNH	British Museum (Natural History)
CAS	California Academy of Sciences
CAS-SU	Stanford University Collection (In California Academy of Sciences)
CM	Carnegie Museum
FMNH	Field Museum of Natural History
KU	University of Kansas Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard University
MIZS	Museo ed Istituto di Zoologi Sistematico, Università di Torino
MJP	Museo Javier Prado, Lima
MNHN	Muséum National d'Histoire Naturelle, Paris
MPEG	Museu Paraense Emiliano Goeldi, Belém
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
MZUSP	Museu de Zoología, Universidade da São Paulo
NHMG	Naturhistoriska Museet Göteborg
NHMW	Naturhistorisches Museum, Wien
NHRM	Naturhistoriska Riksmuseet, Stockholm
RMNH	Rijksmuseum van Natuurlijke Histoire, Leiden
SMF	Senckenbergische Museum, Frankfurt
UIMNH	University of Illinois, Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
UP	Université de Paris
UPR-M	University of Puerto Rico, Mayagüez
UTA	University of Texas, Arlington

USNM	United States National Museum
UZM	Universitets Zoologiske Museum, Copenhagen
WCAB	Werner C. A. Bokermann, São Paulo, Brasil
ZMB	Zoologisches Museum Berlin
ZSM	Zoologisches Sammlung München

HISTORICAL RESUMÉ

Because of the taxonomic confusion that has surrounded the generic name *Osteocephalus* and two of the species (and their synonyms), we present a brief resumé of the taxonomic history of the group.

Among the amphibians sent to the Muséum National d'Histoire Naturelle in Paris by a Monsieur Leprieur in French Guiana was a single female specimen of a moderately large hylid having a well-ossified skull and smooth dorsal skin. This specimen escaped from the covetous eyes of Johann Tschudi, who prematurely named several species on the basis of specimens in Paris, and survived without an epithet until Duméril and Bibron (1841) proposed for it the name *Hyla leprieurii*. The description of the species is fairly detailed, but the specimen was not illustrated. This is the earliest trivial name now associated with *Osteocephalus*.

Fitzinger (1843) in his generic synopsis of amphibians and reptiles proposed the generic name *Osteocephalus* but did not associate a specific name with the genus. Consequently, *Osteocephalus* Fitzinger, 1843, is a *nomen nudum*. Franz Steindachner followed Leopoldo Fitzinger at the Naturhistorisches Museum in Vienna, where he had access to Fitzinger's notes and, of course, the important collections housed in that museum. Steindachner (1862) named two species of *Osteocephalus* on the basis of Brasilian specimens collected by Johann Natterer. Both species were named in the same publication; *O. taurinus* appeared on page 77, and *O. flavolineatus*, on p. 80. This is the earliest association of the generic name *Osteocephalus* with a specific name and a description, both of which satisfy the Code of Zoological Nomenclature for generic availability. Therefore, Steindachner is the authority for the generic name *Osteocephalus*, which has *O. taurinus* as the type species by original designation. It is not possible to determine whether or not Steindachner's usage of *Osteocephalus* was the same as that intended by Fitzinger 19 years earlier.

Steindachner (1862) gave reasonably good descriptions of his two new species and provided excellent illustrations of the two specimens, both large females. Apparently impressed by the similarities between *Trachycephalus nigromaculatus* Tschudi, 1838, and

Osteocephalus taurinus, Steindachner (1867) used the combination *Trachycephalus (Osteocephalus) taurinus*. This ambiguous usage for the 1860's precludes our determining if Steindachner was in effect synonymizing *Osteocephalus* with *Trachycephalus* or whether he was placing *Osteocephalus* in a subgeneric status. Steindachner (1867) did not mention *O. flavolineatus;* perhaps by that time he had concluded that *flavolineatus* was only a color morph of *taurinus*.

Cope (1867) placed *Hyla leprieurii* in the genus *Hypsiboas* Wagler, 1830. Cope (1874) named *Osteocephalus planiceps* from Nauta, Perú. The single specimen was among the collections made by the Orton Expedition to the upper Amazon Basin and was deposited in the Academy of Natural Sciences in Philadelphia.

Boulenger (1882) placed both *Osteocephalus* and *Trachycephalus* is the synonymy of *Hyla;* he recognized *Hyla taurina* (with *O. flavolineatus* as a synonym), *H. leprieurii*, and *H. planiceps*. In the same publication Boulenger named *Hyla buckleyi* on the basis of 10 specimens in the British Museum from Ecuador; in the description he stated that *buckleyi* was like *leprieurii* and *taurinus* in having paired lateral vocal sacs. Boulenger held a lasting influence on taxonomic herpetology, and his generic synonymy of *Osteocephalus* was unchallenged until only a decade ago.

Goin (1961) presented a generic synopsis of the genera of hylid frogs, in which he recognized *Osteocephalus* and stated: "There are perhaps eight or ten species of this genus in South America. Certainly *taurinus*, *britti*, *leprieuri*, *buckleyi* and *pearsoni* belong here. *O. planiceps* is surely a synonym of *leprieuri* and I believe that *garbei* is as well. The status of such forms as *macrotis*, *riopastazae*, and *depressa* has not yet been settled." Goin defined *Osteocephalus* as follows: "Males with paired vocal pouches, one at each angle of the jaw; derm of head not co-ossified with skull but roof of skull exostosed." Trueb (1970a) elaborated on Goin's definition and assuredly included only *O. taurinus* and *O. leprieurii* in the genus.

Goin's inclusion of *buckley*, *britti*, and *pearsoni* in *Osteocephalus* was the first association of any of these names with that genus. Duellman (1970a) demonstrated that *Garbeana garbei* Miranda-Ribeiro, 1926, was a member of the *Hyla rubra* group. *Hyla macrotis* Andersson, 1945, is a *Phrynohyas*. Trueb and Duellman (1970) determined that *Hyla verrucigera* Werner, 1901, is the earliest name for an *Osteocephalus* displaying striking sexual dimorphism in coloration and texture of the dorsal skin; *Hyla riopastazae* Andersson, 1945 (female holotype), and *Hyla orcesi*

Funkhouser, 1956 (male holotype), were placed in the synonymy of *Osteocephalus verrucigerus.*

Hyla pearsoni Gaige, 1929, is a small species of *Osteocephalus.* Our findings substantiate Goin's suggestions relative to two other taxa. *Hyla leprieurii britti* Melin, 1941, from the Rio Uaupés, Brasil, and *Hyla depressa* Andersson, 1945, from the Río Pastaza watershed, Ecuador, are members of the genus *Osteocephalus*, but both are synonyms of earlier names—*leprieurii* and *taurinus*, respectively. Another name proposed by Melin (1941), *Hyla (Trachycephalus) vilarsi* from Taracuá, Brasil, also is placed in the synonymy of *O. taurinus.*

Cochran and Goin (1970) were unaware of the identities of *Hyla verrucigera* and *riopastazae;* they used the later name *Osteocephalus orcesi* for Colombian frogs that are correctly referred to *O. verrucigerus.* Although Goin (1961) placed *Hyla buckleyi* and *H. pearsoni* in *Osteocephalus,* Cochran and Goin (1970) recognized a "*buckleyi* group" in *Hyla* that included these two species plus a new species, *Hyla cabrerai* from Amazonian Colombia and Brasil (total of three specimens). Also, these authors named *Hyla carri* from a single Colombian specimen. Study of the types of *Hyla cabrerai, H. carri,* and *H. festae* Peracca, 1904, from Ecuador, reveal that all of these names are synonyms of *Osteocephalus buckleyi.*

Much of the taxonomic confusion and multiplicity of trivial names is due to the great amount of color variation in *taurinus* and to the sexual dimorphism in the texture of the dorsal skin in all of the species. The details of variation in these and other characters and our justifications for the synonymies are given in the accounts of the species. All of the trivial names that apply to species herein recognized as members of the genus *Osteocephalus* are listed in table 1.

Osteocephalus Steindachner, 1862

Osteocephalus Steindachner, 1862:77 [Type species.—*Osteocephalus taurinus* Steindachner, 1862, by original designation]. Not *Osteocephalus* Fitzinger, 1843:50 *(nomen nudum).*

Diagnostic Definition.—1) Skull broader than long; 2) dermal roofing bones of skull well ossified, exostosed, and/or co-ossified in some species; 3) prenasal and internasal bones absent; 4) parasphenoid alae posterolaterally oriented; 5) dentigerous processes of prevomers angular (／￣＼); 6) vocal sacs paired, posterior, and when inflated protruding posteroventral or posterolateral to angles of jaws; 7) submentalis muscle moderate in size and araphic; 8) intermandibularis muscle undifferentiated and bearing an elongate

TABLE 1.—Alphabetical Synonymy of the Species of *Osteocephalus*.

Trivial Name, Original Generic Name, Author, Date	Current Name
britti (Hyla leprieurii) Melin, 1941	*O. leprieurii*
buckleyi (Hyla) Boulenger, 1882	*O. buckleyi*
cabrerai (Hyla) Cochran and Goin, 1970	*O. buckleyi*
carri (Hyla) Cochran and Goin, 1970	*O. buckleyi*
depressa (Hyla) Andersson, 1945	*O. taurinus*
festae (Hyla) Peracca, 1904	*O. buckleyi*
flavolineatus (Osteocephalus) Steindachner, 1862	*O. taurinus*
leprieurii (Hyla) Duméril and Bibron, 1841	*O. leprieurii*
orcesi (Hyla) Funkhouser, 1956	*O. verrucigerus*
pearsoni (Hyla) Gaige, 1929	*O. pearsoni*
planiceps (Osteocephalus) Cope, 1874	*O. taurinus*
riopastazae (Hyla) Andersson, 1945	*O. verrucigerus*
taurinus (Osteocephalus) Steindachner, 1862	*O. taurinus*
verrucigera (Hyla) Werner, 1901	*O. verrucigerus*
vilarsi (Hyla) Melin, 1941	*O. taurinus*

median aponeurosis; 9) parotoid glands absent or poorly developed, skin not producing viscous secretion characteristic of *Phrynohyas;* 10) skin on dorsum tuberculate in males, smooth in females; 11) tympanum large, 60 percent or more of diameter of eye; 12) fingers about one-third, toes more than three-fourths webbed; 13) discs large, round; 14) nuptial excrescences present in breeding males; 15) inner metatarsal tubercle not modified for digging; 16) outer metatarsal tubercle absent; 17) tarsal fold weak or absent; 18) pupil horizontal; 19) palpebrum clear; 20) known tadpoles having two upper and five lower rows of teeth.

Content.—As defined here, the genus contains five known species: *O. buckleyi* (Boulenger), *O. leprieurii* (Duméril and Bibron), *O. pearsoni* (Gaige), *O. taurinus* Steindachner, and *O. verrucigerus* (Werner).

Distribution.—The Guianas and Amazon Basin; also in the upper Orinoco and Magdalena drainages. Most localities are at elevations below 500 m, but the genus ascends the Amazonian slopes of the Andes to elevations of about 1800 m.

ANALYSIS OF CHARACTERS

Size and Proportions.—Frogs of the genus *Osteocephalus* are moderate to large hylids. The largest species is *taurinus*, attaining a snout-vent length of 103.1 mm; the smallest is *pearsoni*, which attains a length of 54.7 mm. Considerable intraspecific geographic variation occurs in adult size, especially in *taurinus*. Females of all species attain a noticeably larger size than males, but no significant differences are apparent in proportions (Table 2).

TABLE 2.—Comparison of Size and Proportions in the Species of *Osteocephalus*.
(Means are given in parentheses below observed ranges)

Species		*N*	Snout-vent Length	Tibia Length/ S-V L	Foot Length/ S-V L	Head Length/ S-V L	Head Width/ S-V L	Tympanum/ Eye
O. buckleyi	♂	30	37.9-48.1 (43.3)	0.478-0.580 (0.520)	0.375-0.444 (0.408)	0.319-0.357 (0.343)	0.329-0.368 (0.351)	0.608-0.820 (0.711)
	♀	31	48.6-75.1 (61.7)	0.476-0.599 (0.553)	0.363-0.469 (0.428)	0.310-0.358 (0.333)	0.318-0.367 (0.348)	0.574-0.905 (0.734)
O. leprieurii	♂	21	41.2-48.4 (44.7)	0.514-0.571 (0.538)	0.383-0.430 (0.408)	0.308-0.357 (0.335)	0.326-0.368 (0.348)	0.652-0.884 (0.777)
	♀	21	46.6-61.5 (57.1)	0.516-0.592 (0.539)	0.382-0.453 (0.404)	0.314-0.343 (0.329)	0.328-0.363 (0.349)	0.698-0.909 (0.785)
O. pearsoni	♂	2	45.3-46.2 (45.8)	0.481-0.504 (0.493)	0.404-0.437 (0.421)	0.322-0.335 (0.329)	0.327-0.342 (0.335)	0.660-0.673 (0.666)
	♀	1	54.7	0.521	0.405	0.318	0.346	0.862
O. taurinus	♂	59	40.3-84.6 (66.3)	0.512-0.576 (0.541)	0.387-0.445 (0.416)	0.296-0.345 (0.318)	0.301-0.355 (0.324)	0.638-0.896 (0.752)
	♀	45	45.1-103.1 (75.8)	0.520-0.577 (0.542)	0.391-0.448 (0.420)	0.306-0.334 (0.321)	0.308-0.347 (0.327)	0.640-0.817 (0.758)
O. verrucigerus	♂	11	50.4-54.3 (53.0)	0.494-0.552 (0.519)	0.409-0.442 (0.427)	0.322-0.346 (0.333)	0.328-0.344 (0.337)	0.623-0.804 (0.730)
	♀	3	63.1-65.8 (64.5)	0.532-0.561 (0.545)	0.435-0.463 (0.448)	0.345-0.347 (0.346)	0.348-0.379 (0.358)	0.692-0.808 (0.731)

Coloration.—All *Osteocephalus* are predominantly brown frogs usually with some darker dorsal markings (Figs. 1 and 2). *Osteocephalus verrucigerus* has a nearly uniform dark brown dorsum and no distinct transverse bars on the limbs, whereas all of the other species have distinct bars on the limbs. The dorsal markings on the body consist of irregular blotches in *buckleyi*, *pearsoni*, and *taurinus* but are narrow transverse marks in *leprieurii*. A narrow middorsal cream or yellow stripe is present in some individuals of *buckleyi* and *taurinus* but absent in all individuals of the other species. The flanks are uniform pale tan in *leprieurii* and uniform reddish brown in *verrucigerus;* in the other species the flanks are cream to brown with dark brown or black spots (also dark diagonal marks in some *buckleyi*). A creamy white anal stripe is present in some specimens of *leprieurii* but absent in all individuals of other species.

The postocular region, encompassing the tympanum, is dark brown in most specimens. In adults of *pearsoni* and *taurinus* the upper lips are dark brown. A pale cream or tan suborbital spot is present in *pearsoni* and in some *taurinus;* in some specimens of *taurinus* the suborbital spot is expanded posteriorly forming a labial stripe on the posterior part of the lip. The labial markings of *verrucigerus* are similar to the latter pattern, except that in females a distinct, light labial stripe extends the length of the lip. *Osteocephalus leprieurii* has a distinct, broad, pale labial stripe. The lips are barred cream and dark brown in *buckleyi*.

The venter is uniform creamy white or pale tan in *leprieurii*, uniform white in some *buckleyi* (most males), and uniform tan in some *taurinus*. The other species and some individuals of *taurinus* and *buckleyi* (most females) have dark ventral markings. These markings are most distinctive in *verrucigerus*, in which the venter is white with bold black mottling and spots (Fig. 3c). Those individuals of *taurinus* having ventral markings usually have indistinct, diffuse brown spots on the throat and chest (Fig. 3b). *Osteocephalus pearsoni* is characterized by a fine brown reticulation on the venter and on the anterior and posterior surfaces of the thighs in adults (Fig. 3a). Individuals of *buckleyi* that have ventral markings vary between the patterns illustrated for *pearsoni* and *taurinus* (Figs. 3b and c).

Ontogenetic change in coloration is slight or non-existent in *buckleyi*, *pearsoni*, and *taurinus*, except that juveniles lack ventral markings. A dark blotch on the back and distinct transverse bars on the limbs are evident in juveniles of *verrucigerus;* these markings are obscured in the adults. Juveniles of *leprieurii* are olive-brown

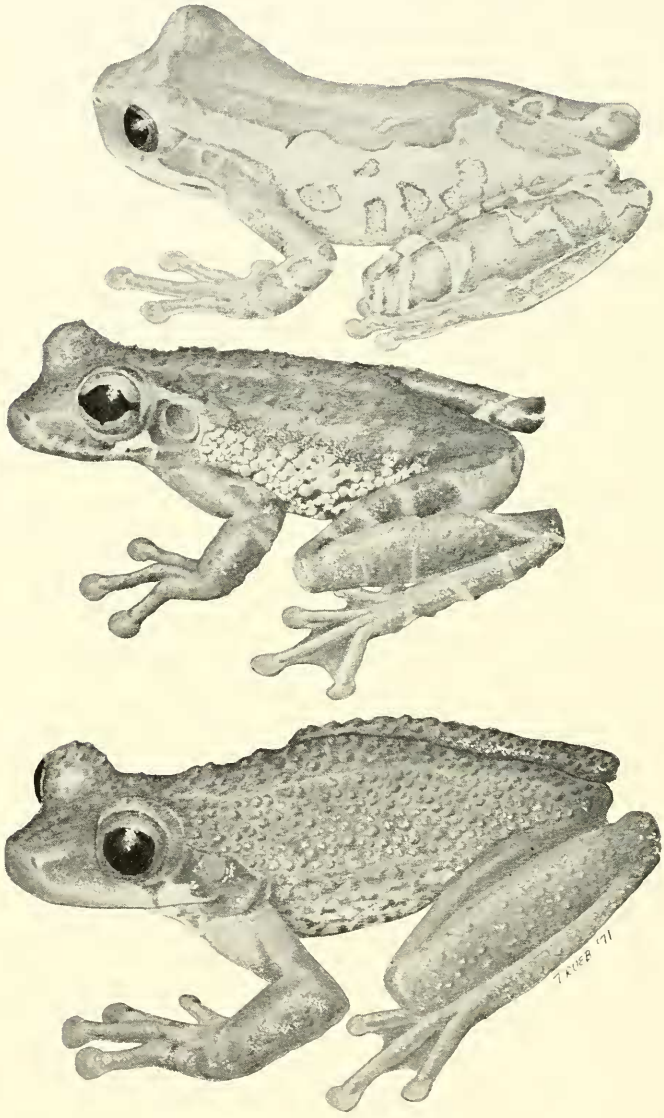

FIG. 1. Species of *Osteocephalus:* Top. *O. pearsoni,* KU 136312, ♂; Middle. *O. buckleyi,* KU 123172, ♂; Bottom. *O. verrucigerus,* KU 123177, ♂. ×1.5.

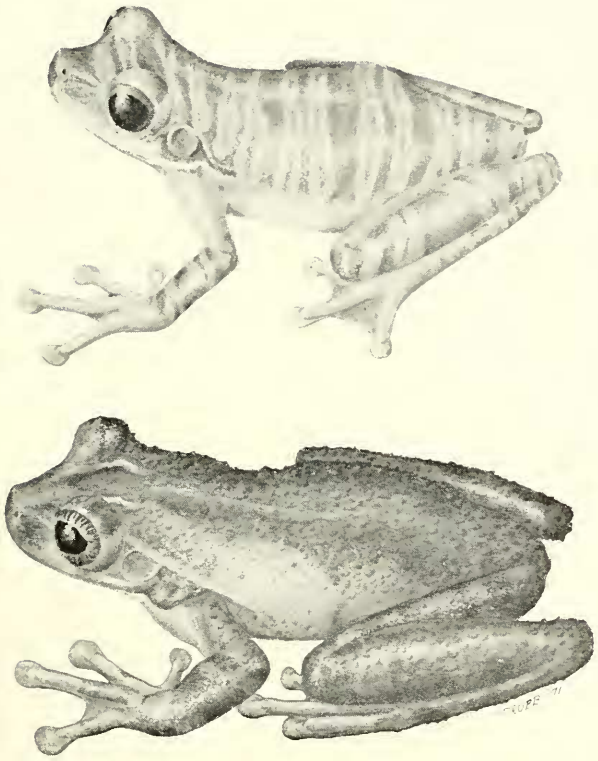

FIG. 2. Species of *Osteocephalus*: Top. *O. leprieurii*, KU 126611, ♀; Bottom. *O. taurinus*, KU 126648, ♂. ×1.

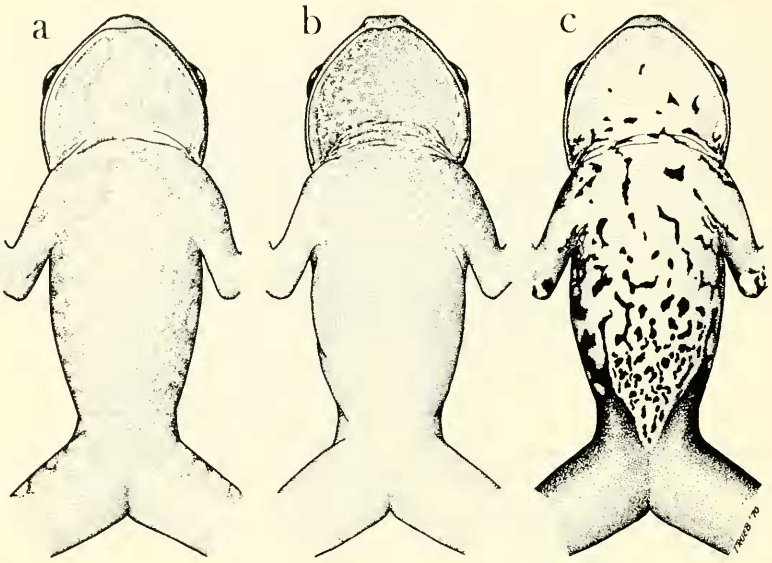

FIG. 3. Diagrammatic views of ventral color patterns in *Osteocephalus:* a. *O. pearsoni,* UMMZ 57533, ♂; b. *O. taurinus,* USNM 166037, ♂; c. *O. verrucigerus,* KU 123185, ♀.

with yellow dorsolateral stripes; the transverse dark marks, characteristic of the adults, appear before the stripes are lost.

Skin.—The dorsal skin of all males of *Osteocephalus* is tuberculate to varying degrees, whereas the dorsal skin of females is smooth, or nearly so (Fig. 4). *Osteocephalus verrucigerus* differs from other members of the genus by the presence of numerous, large tubercles bearing keratinized tips. The tubercles of *leprieurii* are numerous and spinous but much smaller than those of *verrucigerus;* those of *taurinus* are spinous but less numerous than in *leprieurii. Osteocephalus buckleyi* has a mixture of large and small, non-spinous tubercles, and *pearsoni* has only a few, small, scattered, non-spinous tubercles. Fleshy tubercles occur on the eyelids and supratympanic fold in females of *buckleyi;* a few small tubercles are present on the back of females of *pearsoni,* whereas the dorsal skin in females of the other species is smooth. The skin on the flanks of both sexes of *buckleyi* is weakly areolate; in the other species the flanks are smooth. The skin on the top of the head in *taurinus* is rugose as a consequence of co-ossification. In all species the anal opening is directed posteriorly at the upper level of the thighs.

Hands and Feet.—The feet of *Osteocephalus* are fully webbed or

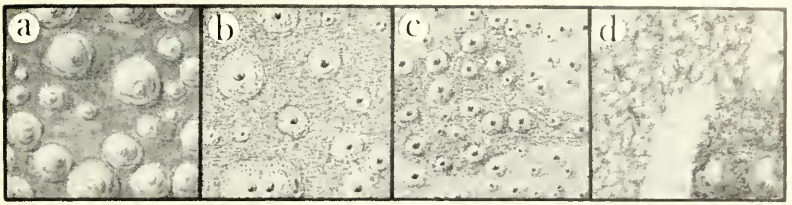

FIG. 4. Segments of dorsal skin of males of *Osteocephalus* showing size and arrangement of tubercles: a. *O. verrucigerus*, KU 123183; b. *O. taurinus*, USNM 166033; c. *O. leprieurii*, KU 126616; d. *O. buckleyi*, USNM 165999. Each square = 1 sq. cm.

nearly so. Webbing between fingers one and two is basal in all species. Webbing between fingers two, three, and four is most extensive in *taurinus*, in which the three fingers are about one-half webbed (Fig. 5). *Osteocephalus buckleyi*, *pearsoni*, and *verrucigerus* have reduced webbing between fingers two and three, and *leprieurii* has reduced webbing between fingers two, three, and four. All members of the genus have well-developed subconical subarticular tubercles on the fingers and toes; there is a tendency for the distal tubercle on the fourth finger to be weakly bifid. Palmar and plantar supernumerary tubercles are well developed in *taurinus*, moderately developed in *buckleyi*, *leprieurii*, and *pearsoni*, and barely evident in *verrucigerus*. All of the species have a noticeable fold on the wrist and enlarged prepollices, bearing horny nuptial excrescences in breeding males. The prepollex is least enlarged in *buckleyi*. Outer metatarsal tubercles are absent. The inner metatarsal tubercle is moderately well developed and ovoid in *leprieurii* and *pearsoni;* it is elliptical and flat in the other species. Tarsal folds are absent in all species except *verrucigerus*, in which the folds are barely evident.

Cranium.—As a genus, the cranial structure is remarkably uniform and quite generalized when viewed in the context of the family Hylidae. The skulls are broad and relatively flat, each being only slightly more broad than long and about one-third as high as long. In dorsal aspect the snouts are broadly rounded; the snout of *buckleyi* is somewhat less rounded and appears to be slightly longer than the snouts of other species. This subtle difference relates to the relative narrowness of the premaxillaries in *buckleyi*.

The genus is characterized by well-developed dermal roofing bones and an unusually large exposure of the sphenethmoid dorsally (Fig. 6). The conformation of the sphenethmoid exposed dorsally is determined by the marginal positions of the adjacent, overlapping

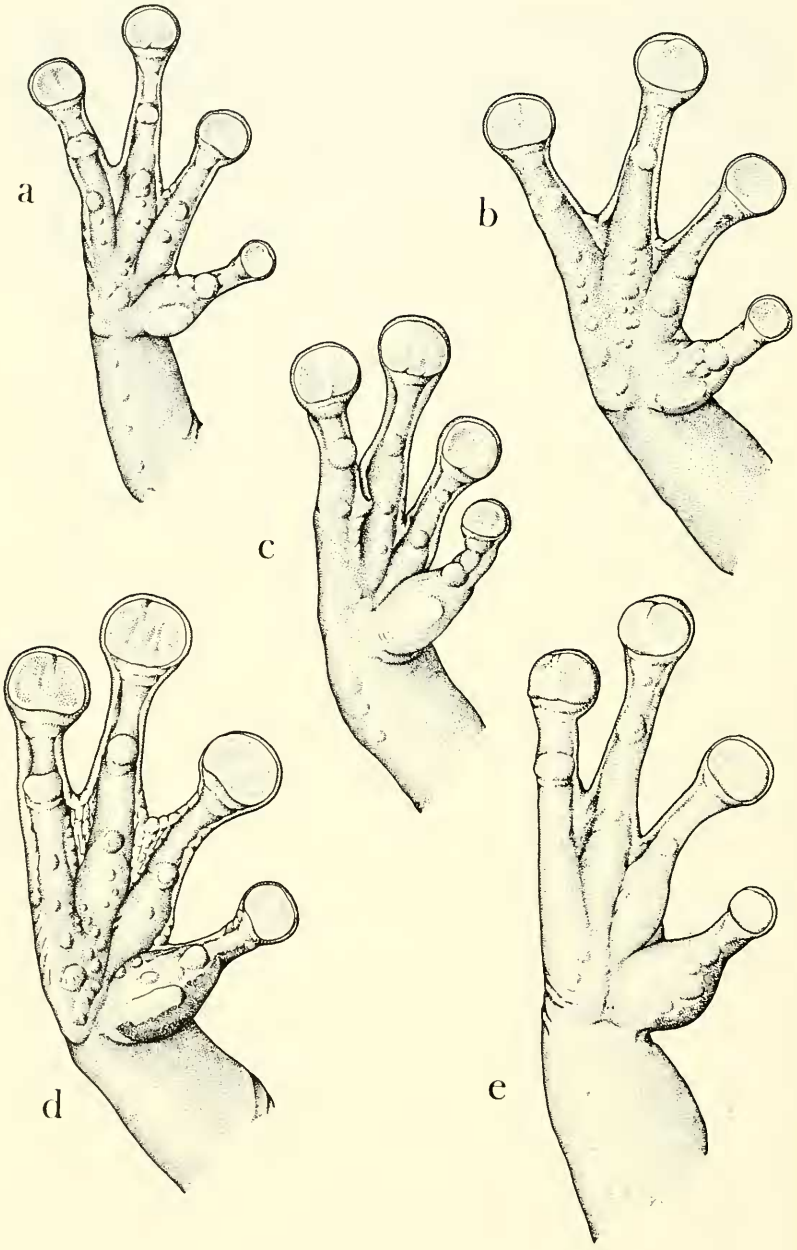

FIG. 5. Palmar views of hands of males of *Osteocephalus:* a. *O. buckleyi,* KU 109506; b. *O. leprieurii,* KU 126627; c. *O. pearsoni,* MCZ 15565; d. *O. taurinus,* KU 126653; e. *O. verrucigerus,* KU 123177. ×4.

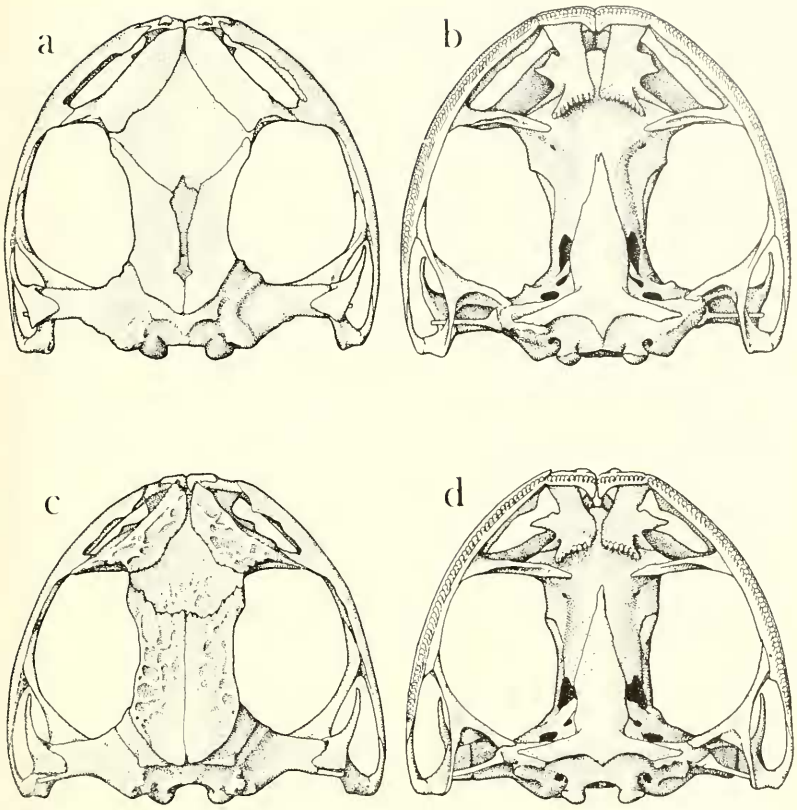

FIG. 6. Skulls of two species of *Osteocephalus:* a and b. *O. leprieurii,* KU 125961; c and d. *O. pearsoni,* UMMZ 67465. ×3.

elements—the nasals and frontoparietals. Medially the nasals overlap the lateral margins of the sphenethmoid. Anteromedially, the nasals converge in *leprieurii* and *taurinus*, are narrowly separated in *buckleyi* and *pearsoni,* or are more widely separated in *verrucigerus.* In all species the nasals terminate at the anterodorsal corner of the orbit. The frontoparietals of *buckleyi, leprieurii,* and *taurinus* have an anterolateral extension, which marginally overlaps the dorsolateral edge of the sphenethmoid and articulates with the posterodorsal corner of the nasal in *buckleyi* and *taurinus;* the bones are narrowly separated in *leprieurii.* The frontoparietals of *pearsoni* and *verrucigerus* have more extensive median ossification and less extensive anterolateral ossification. Thus, in those species the posteromedian portion of the sphenethmoid is obscured, and the

lateral margins are partly exposed. The frontoparietal fontanelle is completely covered in all species, except *buckleyi* and *leprieurii*, in which an irregular, median separation of the frontoparietals exposes a small portion of the fontanelle. The posterolateral margins of the frontoparietals lie medial to the epiotic eminences.

Dermal ornamentation, involving the nasals, frontoparietals, and sphenethmoid, occurs in *taurinus* and, to a limited extent, in *pearsoni*. In the latter species marginal portions of the frontoparietals, the dorsal surfaces of the nasals, and the posteromedial part of the exposed sphenethmoid are slightly exostosed, resulting in an open, reticulate pattern of dermal sculpturing of exceedingly low relief (Fig. 6c). *Osteocephalus taurinus* is characterized by casquing, co-ossification, and a rather intricate pattern of dermal sculpturing, which was described in detail and illustrated by Trueb (1970a).

The squamosals of all species are moderately large structures having otic plates that overlie the lateral portion of the cristae paroticae. The posterior rami are short; the zygomatic rami of all species, except *taurinus*, extend slightly more than one-half of the distance to the maxillary. In *taurinus* the zygomatic ramus extends nearly to, or articulates with, the maxillary.

The maxillary arches are complete and relatively robust. The alary processes of the premaxillaries are vertically oriented in *leprieurii*, *pearsoni*, and *taurinus* and very slightly inclined posteriorly in *buckleyi* and *verrucigerus*. The maxillaries are uniformly characterized by the absence of postorbital processes and by the presence of preorbital processes that articulate with the maxillary processes of the nasals. The partes facialae of the maxillaries are moderately developed in all species, except *taurinus*, in which the pars fascialis tends to articulate with the lateral margin of the nasal in well-ossified individuals. The partes palatinae are poorly developed in all species, except *buckleyi*, in which the pars palatina of the premaxillary is moderately robust.

The pterygoids are uniformly tri-radiate structures. The anterior rami terminate at about the mid-level of the orbit, and the medial rami articulate firmly with the anterolateral corner of the otic capsule. The palatines are well-developed elements bearing ventral ridges; the ridges are somewhat irregular in *buckleyi*, *taurinus*, and *verrucigerus* but smooth in *leprieurii* and *pearsoni*. The parasphenoids are large elements characterized by acuminate cultriform processes and posterolaterally inclined alary processes. The basal areas of the cultriform processes bear small odontoid protuberances in *buckleyi*, *taurinus*, and *verrucigerus*, whereas they are smooth in

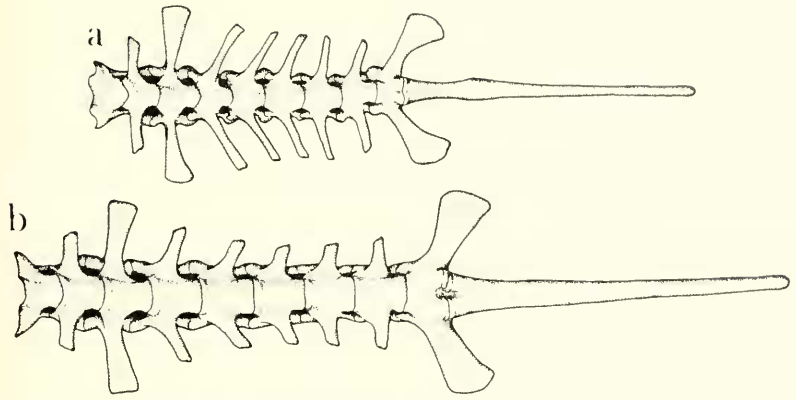

FIG. 7. Dorsal views of vertebral columns of two species of *Osteocephalus:* a. *O. leprieurii,* KU 125962, ♀; b. *O. buckleyi,* USNM 165997, ♀. ×2.

leprieurii and *pearsoni.* The prevomers are remarkably uniform, moderately well-developed structures. In each species the anterior ramus lies adjacent to the premaxillary, and the lateral wings form the anterior, medial, and posteromedial margins of the internal nares. The dentigerous processes are characteristically large and angular and bear numerous teeth. The sphenethmoid and otoccipitals are well ossified; a dermal sphenethmoid is present only in *taurinus.*

Vertebral Column.—The cervical cotyles are uniformly widely displaced. The neural arches are low and non-imbricate. The transverse processes of the third presacral vertebrae are approximately equal in width to the sacral diapophyses in all species, except *buckleyi,* in which the processes of the third presacral are slightly narrower than the diapophyses. *Osteocephalus buckleyi* is further distinguished by the presence of narrow transverse processes on presacrals five through eight (Fig. 7b); males have narrower processes than do females. The processes are moderately wide but subequal in width in *pearsoni, taurinus,* and *verrucigerus,* whereas they are nearly equivalent in width to one another and to the sacral diapophyses in *leprieurii* (Fig. 7a). The scaral diapophyses of all species are moderately dilated and posterolaterally inclined. The coccyx bears a distinct dorsal ridge and has a bicondylar articulation with the sacrum.

Pectoral Girdle.—The pectoral girdles are fully arciferal and bear small, cartilaginous omosterna and moderately large cartilaginous sterna. The coracoids are robust, and the clavicles are strongly arched. Procoracoid cartilage seems to be absent. The

scapulae are large, longer than the clavicles, and bicapitate proximally. The suprascapulae are moderately large and well ossified in *leprieurii* and *taurinus*. The suprascapula of *verrucigerus* is poorly ossified, and that of *buckleyi* is not ossified.

Pelvic Girdle.—The ilia of *buckleyi, taurinus,* and *verrucigerus* lack any indication of a crest on the shaft, whereas *leprieurii* has a low crest. The dorsal acetabular expansion of the ilia is moderately low in *taurinus* and *verrucigerus,* but distinctly lower in *buckleyi* and *leprieurii*. The ilia of all species bear low dorsal protuberances. The ischia of *leprieurii, taurinus,* and *verrucigerus* are moderately expanded; that of *buckleyi* is somewhat less expanded dorsally. The pubis of *leprieurii, taurinus,* and *verrucigerus* are calcified, whereas that of *buckleyi* remains cartilaginous.

Throat Musculature and Vocal Sac Structure.—Tyler (1971) described the throat myology of *Osteocephalus*. The genus is characterized by a moderate-sized araphic submentalis muscle and an undifferentiated intermandibularis having an elongate median aponeurosis. The intermandibularis and submentalis are completely independent in *buckleyi,* whereas in the other species there is a small attachment between these muscles.

According to Tyler (pers. com.), *Osteocephalus* has three distinctive types of vocal sac structure which result from differences in the development of the interhyoideus muscle and the overlying skin. In *leprieurii* and *verrucigerus* the supramandibular portions of the interhyoideus form a simple tubular, posterolateral extension; there is no modification of the associated skin. *Osteocephalus buckleyi* and *pearsoni* have more extensive development of the supramandibular portions of the interhyoideus; furthermore, the associated skin forms a broad, loose fold extending from the ventromedial surface of the throat dorsolaterally to the base of the supratympanic fold. Like *buckleyi* and *pearsoni,* the supramandibular portion of the interhyoideus is much expanded in *taurinus*. The vocal sac structure of *taurinus* differs from that of other members of the genus in that the skin of *taurinus* forms an everted pouch, which dangles loosely beneath the supratympanic fold.

Key to the Species of *Osteocephalus*

1. Inner edge of third finger webbed to mid-length of antepenultimate phalange; dorsum brown with dark brown spots or median blotch; skull in adults casqued and co-ossified with prominent supraorbital flanges ..... *O. taurinus*

Inner edge of third finger webbed to base of antepenultimate phalange; dorsum plain or marked with dark blotches or transverse bars; skull in adults smooth or slightly exostosed, lacking supraorbital flanges 2

2. Skin on flanks areolate; dorsum in males bearing a mixture of large and small non-spinous tubercles; lips distinctly barred ..... *O. buckleyi*

   Skin on flanks smooth; dorsum in males bearing tubercles of uniform size; lips not barred 3

3. Dorsal pattern consisting of narrow transverse dark bars; dorsum in males bearing numerous small spinous tubercles ..... *O. leprieurii*

   Dorsal pattern not consisting of transverse bars; dorsal tubercles large or few in number 4

4. Dorsum uniformly dark brown; venter heavily mottled with black, especially in females; dorsum in males bearing large, keratinized tubercles ..... *O. verrucigerus*

   Dorsum tan with irregular dark brown blotches; venter cream with fine brown reticulations; dorsum in males bearing few, small non-spinous tubercles ..... *O. pearsoni*

Accounts of Species

Osteocephalus buckleyi (Boulenger)

Hyla buckleyi Boulenger, 1882:362 [Syntypes.—BMNH 1947.2.13.36-39 from Sarayacu, Provincia Pastaza, Ecuador; BMNH 1947.2.13.40-41, 1947.2.13. 43-45 from Canelos, Provincia Pastaza, Ecuador; BMNH 1947.2.13.46 from "Paitanga" (= Pallatanga), Provincia Chimborazo, Ecuador (in error); Mr. Buckley collector; BMNH 1947.2.13.44 here designated as lectotype].

Hyla festae Peracca, 1904:39 [Holotype.—MIZS 2950 from "Valle de Santiago" (= lower Río Zamora), Provincia Morona-Santiago, Ecuador; Enrico Festa collector]. New synonymy.

Osteocephalus buckleyi—Goin, 1961:13.

Hyla carri Cochran and Goin, 1970:211 [Holotype.—FMNH 69702 from Acevedo, Río Suaza, Departamento Huila, Colombia; Philip Hershkovitz collector]. New synonymy.

Hyla cabrerai Cochran and Goin, 1970:215 [Holotype.—USNM 152759 from Caño Guacayá, tributary of lower Río Apoporis, Comisaria Amazonas, Colombia; Isadore Cabrera collector]. New synonymy.

Justification of Synonymy.—Boulenger (1882:362) listed 11 specimens in his description of *Hyla buckleyi.* We have examined all of these and conclude that one (BMNH 1947.2.13.42) is *O. leprieurii.* Cochran and Goin (1970:213) restricted the type locality to Canelos, Provicia Pastaza, Ecuador; we here select BMNH 1947.2. 13.44 from that locality as the lectotype. This specimen is a male having a snout-vent length of 37.9 mm; the diameter of the tym-

panum is 3.5 mm, 81.4 percent of the diameter of the eye. The type series, exclusive of BMNH 1947.2.13.42 *(= O. leprieurii)* consists of six males having snout-vent lengths of 37.9-44.6 (mean 40.4) mm, and four females having snout-vent lengths of 50.0-53.9 (mean 51.5) mm. The dorsum in the males bears a mixture of large and small tubercles, whereas the dorsum in females is nearly smooth. The skin on the flanks, especially the axilla, is areolate. The coloration consists of a creamy tan ground color with irregular reddish brown markings on the back and broad transverse bars on the limbs. The dorsal markings are narrowly bordered by creamy white; those on the back consist of an interorbital bar and a pair of longitudinal marks beginning in the scapular region and usually diverging posteriorly in the sacral region or converging into a broad median blotch. One specimen has a middorsal creamy white stripe from the tip of the snout to the vent. In all of the types large dark brown spots are present on the flanks and posterior surfaces of the thighs. The ventral surfaces are pale creamy tan with or without diffuse brown spots on the throat and chest.

The holotype of *Hyla festae* is a female having a snout-vent length of 75.0 mm; the diameter of the tympanum is 3.9 mm, 57.4 percent of the diameter of the eye. The skin is smooth on the dorsum and areolate on the anterior part of the flanks. The dorsum is pale brown with a large median longitudinal dark brown blotch on the back and broad transverse bars, narrowly outlined by cream, on the limbs. Dark brown spots are present on the flanks; the posterior surfaces of the thighs are dark brown. The throat and belly are grayish white with irregular dark brown spots.

The holotype of *Hyla carri* is a female having a snout-vent length of 66.1 mm; the diameter of the tympanum is 4.7 mm, 81.0 percent of the diameter of the eye. The skin on the dorsum is smooth with scattered small tubercles and areolate on the anterior part of the flanks. The dorsum is tan with irregular dark brown blotches on the back and transverse bars on the limbs; all dorsal markings are narrowly outlined by creamy white. Dark brown spots are present on the flanks; the venter and posterior surfaces of the thighs are tan without dark spots.

The holotype of *Hyla cabrerai* is a female having a snout-vent length of 52.7 mm; the diameter of the tympanum is 4.0 mm, 76.9 percent of the diameter of the eye. The skin on the dorsum is weakly tuberculate and that on the anterior part of the flanks is areolate. The dorsum is creamy tan with dark brown markings (interorbital bar, reticulations on occiput, three longitudinal streaks on back,

and broad transverse bars on limbs). Irregular dark brown spots are present on the flanks. The venter is pinkish tan with small reddish brown spots on the throat and darker brown spots on the chest and belly.

In their description of *Hyla cabrerai*, Cochran and Goin (1970: 217) stated: "This species, together with *buckleyi* and *pearsoni* certainly make a closely knit group. . . . Both *buckleyi* and *cabrerai* have long hind legs, with the extended heel reaching to the tip of the snout, while in *pearsoni* the extended heel reaches only to the eye. *H. buckleyi* has the belly dusky, while it is heavily spotted in *cabrerai* and is reticulated in *pearsoni*. *H. cabrerai* seems to have the heaviest hands with the most webbing between the fingers; the other two species have the webbing reduced between the fingers." The description of *Hyla cabrerai* was based on three specimens. We have examined the holotype and one paratype (WCAB 13284 from Territorio do Amapá, Brasil). Another paratype in the private collection of C. J. Goin from Caño Tuí, between Mitú and Raudal de Yurupari, Comisaria de Vaupés, Colombia, was not examined.

Cochran and Goin (1970:211) based their description of *Hyla carri* on one gravid female and stated: "A large *Hyla* with the vomerine teeth in two ∧∧ shaped patches between the somewhat squarish choanae; reduced webs between the fingers; and a pattern of dorsal dark blotches bordered by light margins. The species is not similar to any other species known in Colombia. It is perhaps most closely related to *Hyla claresignata* of Brazil, from which it can be differentiated by its more heavily spotted dorsum, larger tympanum, and lack of dark anal spots."

Except for the inclusion of the name in checklists, *Hyla festae* has not been mentioned in the literature since the original description.

The wholesale synonymization of names, which, on the bases of their published diagnoses, seem to apply to distinctly different species, is possible with the application of uniform criteria to the types and series of other specimens. In measurements and proportions the type specimens of the nominal taxa all fall within the range of variation exhibited by a series of 18 males and 15 females from Provincia Pastaza, Ecuador, except the ratio of the diameter of the tympanum to that of the eye in the female holotype of *Hyla festae*. In that specimen the ratio is 0.574, whereas the ratio in the 15 females from Provincia Pastaza is 0.587-0.905 (mean 0.736).

Ventral coloration is the most variable character among the types. The venter in the type of *Hyla festae* is boldly spotted; it is

distinctly spotted in *cabrerai*, uniform tan in *carri*, and tan, flecked, or spotted in the type series of *buckleyi*. The ventral coloration in series of specimens from Amazonian Ecuador encompasses that observed in all of the types, except that of *festae*, which has more ventral spotting than any other individual.

The webbing on the hand usually excludes the penultimate phalanges of the fingers, but in some specimens from Amazonian Ecuador the webbing encompasses the proximal parts of the penultimate phalanges of the fingers. In a few of these specimens, the holotype of *festae*, and one paratype of *cabrerai* the webbing extends to the middle of the penultimate phalanges of the third and fourth fingers. In the holotype of *cabrerai* the webbing extends to the middle of the penultimate phalanges of the third and fourth fingers and to the base of the disc of the second finger.

The types of the nominal taxa and series of specimens from Guyana and Amazonian Ecuador display noticeable variation in dorsal coloration. The variety of dorsal patterns of all of the types is included in the variation displayed by the other specimens. All specimens have some amount of dark spotting on the flanks; all have vertically barred lips, on which a pale subocular spot usually is evident. Probably the most unifying physical characteristic of all of the specimens is the nature of the skin on the anterior part of the flank. The skin is elevated amidst an irregular network of depressions. This areolate dermal condition is present in all specimens and does not occur in other species of *Osteocephalus*. The degree of tubercularity of the skin on the dorsum is variable and sexually dimorphic. All males are tubercular, whereas small females are smooth or have only a few scattered tubercles. Large females usually have pronounced tubercles on the eyelids and supratympanic fold.

In their description of *Hyla carri*, Cochran and Goin (1970:211) misrepresented the nature of the dentigerous processes of the prevomers, which are angular, not ∧-shaped. Their suggestion that the Colombian *Hyla carri* is related to *Hyla claresignata* in southeastern Brasil is unfounded. The latter species is smaller (40 mm), has a yellow dorsum and venter, dark brown spots dorsolaterally, oblique dentigerous processes of the prevomers, small tympanum, and smooth skin dorsally.

The ventral coloration of the type of *Hyla festae* resembles that of *Osteocephalus verrucigerus*, but the type differs from *verrucigerus* by having areolate skin on the flanks and distinct dark markings on the dorsum. In *verrucigerus* the skin on the flanks is smooth,

and the dorsum is uniform dark brown, except for a tan snout in females.

Comparisons of the types of the nominal species with series of specimens from Guyana, Colombia, Ecuador, and Perú suggest strongly that the types are representative of one taxon, the oldest name for which is *Hyla buckleyi* Boulenger, 1882. Consequently, we place *Hyla festae* Peracca, 1904, *Hyla carri* Cochran and Goin, 1970, and *Hyla cabrerai* Cochran and Goin, 1970, as junior synonyms of *Hyla buckleyi* Boulenger, 1882.

Diagnosis.—1) Size moderate, sexual dimorphism extreme; maximum observed snout-vent length in males 48.1 mm, in females 75.1 mm; 2) skin on dorsum in males bearing a mixture of large and small non-spinous tubercles; 3) skin on flanks, especially anteriorly, areolate; 4) web usually extending only to base of antepenultimate phalange on inner edge of third finger; 5) dorsum pale tan or green with irregular, longitudinal, dark brown blotches, usually narrowly outlined with cream; 6) venter cream or tan, suffused with brown or marked with brown spots in some specimens; 7) lips marked with vertical brown and cream bars; 8) flanks creamy tan with irregular brown spots and/or diagonal marks; 9) dermal roofing bones of skull lacking exostosis; 10) dermal sphenethmoid absent; 11) nasals widely separated medially; 12) anteromedial margin of frontoparietal at mid-level of orbit; 13) frontoparietal fontanelle partially exposed; 14) palatine serrate; 15) parasphenoid bearing odontoids; 16) zygomatic ramus of squamosal extending approximately one-half of distance to maxillary arch; 17) transverse processes of third presacral vertebra narrower than sacral diapophyses; transverse processes of presacral vertebrae 3-8 subequal in width and narrower in males than in females; 18) intermandibularis and submentalis muscles independent; 19) supramandibular portion of interhyoideus extensively developed; associated skin forming broad loose fold.

Osteocephalus buckleyi can be distinguished readily from all other species in the genus by the presence of areolate skin anteriorly on the flanks and by the rather boldly contrasting dorsal pattern. Furthermore, females are distinctive in having tubercles on the eyelids and supratympanic folds.

Distribution.—The periphery of the Amazon Basin, in the Guianas and Territorio do Amapá in northeastern Brasil; the upper Amazon Basin from southern Colombia to east-central Bolivia; one locality (Acevedo) in upper Río Magdalena drainage in Colombia (Fig. 8). All localities are at elevations of less than 700 m. Records

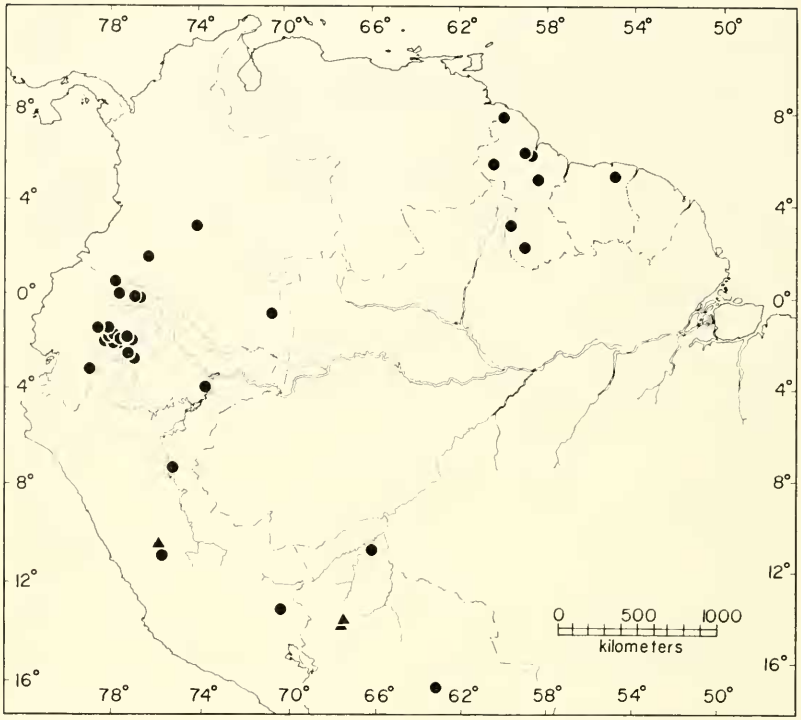

FIG. 8. Distribution of *Osteocephalus buckleyi* (circles) and *O. pearsoni* (triangles).

for Pallatanga and Santiago in Provincia Chimborazo, Ecuador (high on the Pacific slopes of the Andes), are considered to be erroneous. 78 specimens from 40 localities.

Remarks.—In life the dorsum is green with dark markings. A male (KU 123171) from Santa Cecilia, Ecuador, was: "Dorsum green with dark brown blotches. Anterior and posterior surfaces of thighs dull blue. Venter brown, flecked with white. Iris greenish bronze with brown horizontal triangles and ventromedian brown line." (W. E. Duellman, field notes, 16 June 1968.) A female (KU 126646) from Lago Agrio, Ecuador, was: "Dorsum pale green with darker green blotches and creamy yellow middorsal stripe. Lateral blotches bronze-tan. Flanks tan with black blotches. Anterior surfaces of thighs dark brown. Dorsal and posterior surfaces of thighs and shanks tan with dark brown blotches. Webbing brown. Suborbital spot green. Postorbital bar black. Belly grayish brown in appearance—tips of granules white; intergranular spaces brown. Iris golden bronze with black flecks peripherally and median, hor-

izontal, reddish brown streak." (W. E. Duellman, field notes, 12 May 1969.)

No ontogenetic change in coloration has been noted.

Osteocephalus leprieurii (Duméril and Bibron)

Hyla leprieurii Duméril and Bibron, 1841:553 [Holotype.—MNHN 4629 from "Cayenne"; Mons. Leprieur collector].
Hypsiboas leprieurii—Cope, 1867:200.
Hyla leprieurii britti Melin, 1941:42 [Holotype.—NHMG 489 from the Rio Uaupés, north of the Rio Japu, Territorio do Amazonas, Brasil; Douglas Melin collector]. New synonymy.
Hyla leprieurii leprieurii—Melin, 1941:42.
Osteocephalus britti—Goin, 1961:13.
Osteocephalus leprieurii—Goin, 1961:13.

Justification of Synonymy.—The holotype of *Hyla leprieurii* is a female having a snout-vent length of 46.6 mm. The diameter of the tympanum is 3.7 mm, 69.8 percent of the diameter of the eye. The dorsal roofing bones are smooth, and the skin on the dorsum is smooth. The penultimate phalanges of the fingers are not included in the webbing. When we examined the specimen on 2 July 1969, it was slightly soft and somewhat faded to a peculiar grayish green color with faint darker transverse bars on the limbs. Duméril and Bibron (1841:554) described the coloration, as follows: "The loreal region in black. A stripe of the same color extends from the posterior border of the orbit to the corner of the mouth, passing through the tympanum. All of the dorsal parts are grayish white with large transverse brown bands, which are more expanded and less regularly outlined on the back than on the limbs. There is one of these on the occiput that is in a triangular shape. All of the venter is white." (Free translation from French.)

The holotype of *Hyla leprieurii britti* is a male having a snout-vent length of 48.1 mm. The diameter of the tympanum is 3.6 mm, 65.5 percent of the diameter of the eye. The skin on the dorsum is tubercular; the tubercles are small on head and on the dorsal surfaces of the limbs and slightly larger on the back. The penultimate phalanges of the fingers are not included in the webbing. Melin (1941:43) stated: "Above blackish brown with a very indistinct band between the eyes; iris with mottle of metalic lustre; hinder parts of upper jaw whitish; sides of body mottled with blackish brown; hind limbs (especially tibiae and tarsi) with narrow, diffuse cross bars; beneath whitish with slight brown mottle along jaw." We examined the type on 17 February 1969; at that time it was dull brown above with faint, narrow, dark brown, transverse bars on

the back and dorsal surfaces of the limbs. A cream subocular spot was evident, and the venter was creamy white.

Melin (1941:42) stated that the holotype of *Hyla leprieurii britti* ". . . resembles a good deal *H. leprieurii* Dum. & Bibr. As, however, it differs from the latter species by its very concave loreal region, small tympanum, and almost uniformly brownish colour, it may at least form a subspecies of *leprieurii* . . ." The pattern of narrow transverse bars on the backs of the holotypes of *H. leprieurii* and *H. britti* is a condition shared only by these two nominal taxa that are placed in *Osteocephalus.* Melin noted that *britti* differed from *leprieurii* in the depth of the loreal concavity and in the size of the tympanum. Neither of these differences is noteworthy in comparison with series of specimens. The depth of the loreal concavity is a highly subjective character, and we note no differences between the types. The ratio of the diameter of the tympanum to the diameter of the eye is relatively smaller in both holotypes (0.698 in *leprieurii*—♀; 0.655 in *britti*—♂) than in series of fresh specimens from Lago Agrio, Ecuador (0.652-0.884, mean 0.785 in 17 males; 0.700-0.909, mean 0.790 in 20 females). The smaller proportions in the types may be due to geographic variation or to shrinkage as a result of many years in preservative (130+ years for *leprieurii;* 45 for *britti*).

Comparisons of the holotypes with series of specimens from Ecuador, Guyana, and Surinam indicate that one morphological species occurs throughout the upper Amazon Basin and the Guianas and that both type specimens are representatives of one species. Consequently, we consider *Hyla leprieurii* Duméril and Bibron, 1841, to be a monotypic species with *Hyla leprieurii britti* Melin, 1941, as a junior synonym.

In their account of *Osteocephalus leprieurii,* Cochran and Goin (1970:323) stated: "The specimen described and illustrated (MCZ 28042) has been directly compared with the types of *leprieurii, planiceps,* and *vilarsi* by the junior author and there seems to be no doubt that all are conspecific. Another specimen (CNHM 69716) has been directly compared with the types of *planiceps* and *vilarsi* and these, likewise, are considered conspecific." With this justification Cochran and Goin (1970:322) included *Osteocephalus planiceps* Cope, 1874, and *Hyla vilarsi* Melin, 1941, in the synonymy of *Osteocephalus leprieurii.*

We do not concur with Cochran and Goin's synonymy and contend that *planiceps* and *vilarsi* are synonyms of *Osteocephalus taurinus;* we give our reasons in the account of that species. We have examined the specimens listed as *O. leprieurii* by Cochran and

Goin; several of them, including CNHM (= FMNH) 69716, are *taurinus*. Thus, due to Cochran and Goin's confusion of two taxa, their comparisons of certain specimens with types has little meaning.

Cochran and Goin did not include *Hyla leprieurii britti* in their synonymy of *Osteocephalus leprieurii* but did discuss the name in their account of *Osteocephalus orcesi* (= *O. verrucigerus*), as follows (1970:319): "When we first examined one of the specimens we felt sure that we had Melin's *Hyla britti* at hand, but on direct comparison with the type of *britti* the two proved to be different. After studying the type of *orcesi* (SUNHM 13150) we have no doubt that the specimens at hand are *orcesi* and that *britti* is a different, probably valid species."

Diagnosis.—1) Size moderate, sexual dimorphism evident; maximum observed snout-vent length in males 48.4 mm, in females, 61.5 mm; 2) skin on dorsum in males bearing numerous, minute, spinous tubercles; 3) skin on flanks smooth; 4) web extending to base of antepenultimate phalange on inner edge of third finger; 5) dorsum tan or olive-brown with transverse brown or olive bars; 6) venter creamy white or pale tan without markings; 7) lips marked with creamy tan labial stripe and suborbital spot; 8) flanks pale tan with no markings; 9) dermal roofing bones of skull lacking exostosis; 10) dermal sphenethmoid absent; 11) nasals juxtaposed medially; 12) anteromedial margin of frontoparietal between mid- and anterior levels of orbit; 13) frontoparietal fontanelle partially exposed; 14) palatine not serrate; 15) parasphenoid lacking odontoids; 16) zygomatic ramus of squamosal extending about one-half of distance to maxillary arch; 17) transverse processes of presacral vertebrae 3-8 about equal in width to one another and to sacral diapophyses; 18) intermandibularis and submentalis muscles connected; 19) supramandibular portion of interhyoideus forming simple tubular posterolateral extension; associated skin unmodified.

Osteocephalus leprieurii differs from all other members of the genus by having transverse dark bars on the back. Two other hylids (*Hyla lanciformis* and *multifasciata*) in the Amazon Basin have transverse dark marks on the dorsum. Both of these differ from *leprieurii* by having pointed snouts, much longer hind limbs, and smooth skin dorsally.

Distribution.—The periphery of the Amazon Basin, in the Guianas and the upper part of the basin in southern Colombia, Ecuador, Perú, and extreme western Brasil (Fig. 9). Most localities are at elevations of less than 500 m, but the species ascends the lower

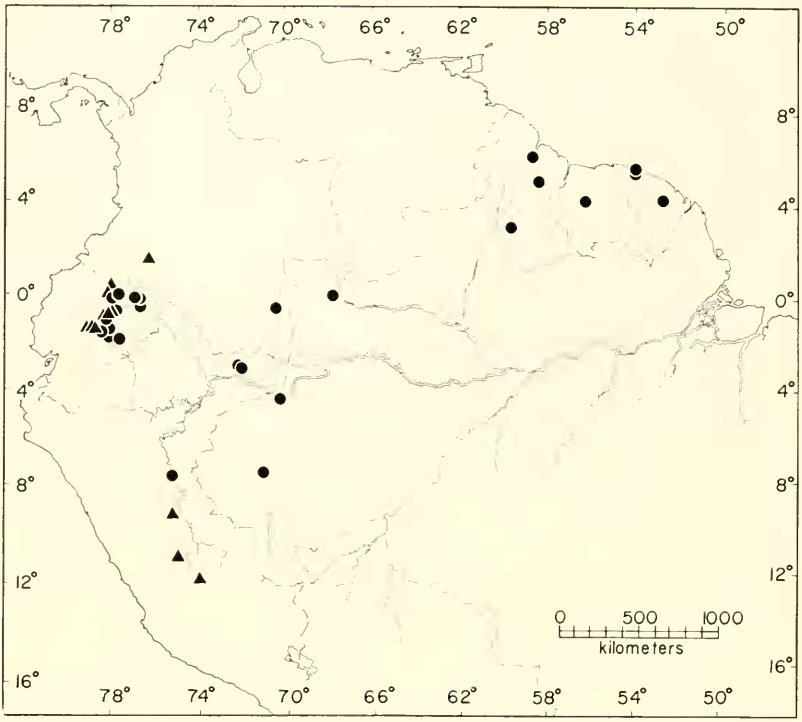

FIG. 9. Distribution of *Osteocephalus leprieurii* (circles) and *O. verrucigerus* (triangles).

Andean slopes to elevations of 1100 m. 265 specimens from 31 localities.

Remarks.—Most adults of *leprieurii* have distinct transverse markings on the back; these are variable in width, extent, and arrangement. In some specimens, such as USNM 166557, some of the transverse bars are fragmented into spots; in a few specimens the dorsal pattern consists solely of small dark spots arranged in transverse rows. Such specimens have a dorsal pattern resembling that of some *taurinus*. The transverse nature of the dorsal markings is further modified in some specimens, such as USNM 166555, in which the dark bars are fragmented and oblique.

Extreme ontogenetic change in color pattern is exhibited by this species (Fig. 10). Juveniles having snout-vent lengths of less than 28 mm have an olive-brown dorsum with a pale cream stripe across the head and broad, cream, dorsolateral stripes; transverse dark bars are absent on the body and limbs. Individuals having snout-vent lengths of 30-35 mm have dark brown transverse bars on

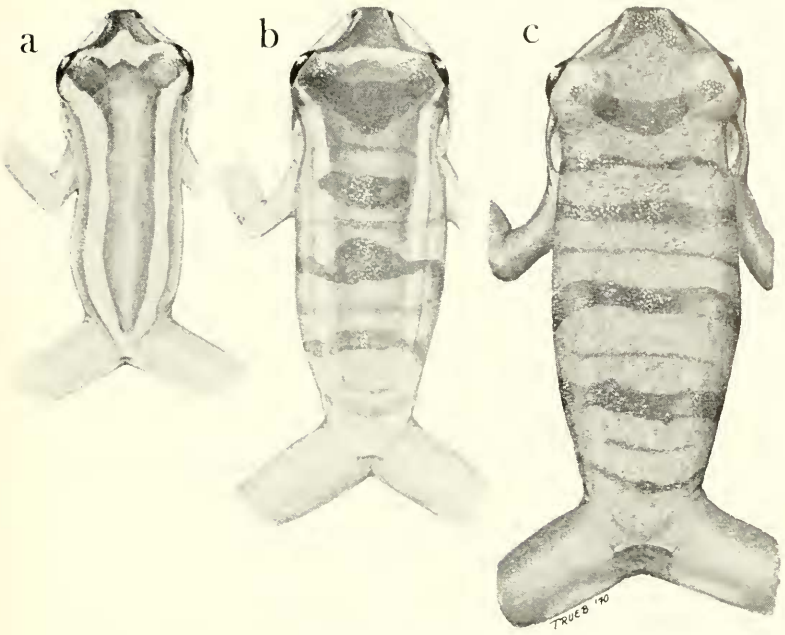

FIG. 10. Ontogenetic change in color pattern in *Osteocephalus leprieurii:* a. KU 126644; b. KU 126640; c. KU 126625. ×2.

the back and limbs but still retain the light dorsolateral stripes, whereas the stripes are lost in larger individuals.

Coloration in life of specimens from Lago Agrio, Ecuador: "In males the dorsal ground color varies from dark brown to ochre-tan; dorsal markings uniformly dark brown. Most specimens have dark brown and cream anal stripes; labial area cream-colored. Flanks vary from tan to white. Ventral coloration varies from salmon to tan to white. The iris is bronze with a greenish cast and black reticulations. In females the dorsal coloration is the same as in males, except that dark marks tend to be outlined with cream; venter tannish salmon." (W. E. Duellman, field notes, 12 May 1969).

Osteocephalus pearsoni (Gaige)

Hyla pearsoni Gaige, 1929:3 [Holotype.—UMMZ 57548 from the upper Río Beni, below mouth of Río Mapiri, Departamento El Beni, Bolivia; N. E. Pearson collector].

Osteocephalus pearsoni—Goin, 1961:13.

Justification of Synonymy.—Goin (1961:13) suggested that *Hyla pearsoni* Gaige was an *Osteocephalus,* but Cochran and Goin (1970: